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OBSERVATIONS ON HOMOLOGIES OF IDIOSOMAL SETAE IN ZERCONIDAE (ACARI: MESOSTIGMATA), WITH MODIFIED NOTATION FOR SOME POSTERIOR BODY SETAE

by Evert E. LINDQUIST* and Maria L. MORAZA**

SUMMARY: The holotrichous condition for the idiosomal chaetotaxy of Zerconidae is reviewed. Using ontogenetic patterns of body setation of holotrichous taxa in other families of Gamasina for comparison, the homologies and notation for some of the podonotal and opisthosomal setae of zerconid mites are changed. These modifications lead to new interpretation of some of the apomorphic attributes used to characterize the family Zerconidae and superfamily Zerconoidea. The caudodorsal displacement of a pair of opisthogastric setae, JV5, so as to appear to be captured by the opisthonotal shield in deutonymphs and adults, is seen to be a unique characteristic of Zerconoidea. The caudal coalescence of the opisthonotal and opisthogastric shields, and the anterior displacement of setae J5 to a nearly transverse alignment with setae Z4 well ahead of the caudal body margin, characterize Zerconidae.

RESUMEN: Se revisa la condición holotrica de la quetotaxia del idiosoma de Zerconidae. Utilizando por comparación los modelos ontogénicos de la quetotaxia del cuerpo determinada para los taxa holotrichos en otras familias de Gamasina, se modifican las homologías y nomenclatura de algunas de las setas podonotales y opistonotales de los ácaros zerconidos. Estas modificaciones llevan a una nueva interpretación de alguno de los atributos apomórficos utilizados en la caracterización de la familia Zerconidae y la superfamilia Zerconoidea. El desplazamiento caudodorsal de un par de setas opistogastricas, JV5, que parecen ser capturadas por la placa opistonal en las deutoninfas y adultos, parece ser una característica única de Zerconoidea. La coalescencia caudal de las placas opistonotal y opistogastrica y el desplazamiento anterior de las setas J5 hasta alcanzar casi un alineamiento transversal con las setas Z4, bien adelantadas respecto al margen caudal del cuerpo, caracteriza a Zerconidae.


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opisthonal des deutonymphes et des adultes, est considéré comme un caractère unique des Zerconoidea. Les Zerconoidea sont caractérisés par la coalescence caudale des boucliers opisthonal et opisthogastrique et par le déplacement antérieur des poils J5 jusqu'à un alignement transversal avec les poils Z4 bien en avant du bord caudal du corps.

**INTRODUCTION**

When Sellnick (1958) published his founding revision of Zerconidae 40 years ago, four genus-group taxa were recognized. Since then, an additional 36 genus-group categories have been proposed, most of them during the nine-year period 1976-1984. Many of these genera are defined primarily on chaetotaxy. These distinctions, however, are sometimes vague, as different systems of setal notation have been used by various authors in description of zeronid mites. Also, interpretations of setal homologies have differed among authors even when using the same system of notation. These disparities have hampered comparisons of the chaetotaxy not only among the genera of this family but also of Zerconidae as a whole with those of other families of Gamasina.

Two systems of notation are currently in widespread use for denoting the idiosomal setae of moustigmatic mites, one developed by Hirschmann (1957) and the other by Lindquist & Evans (1965). Both systems are modifications of a previous one initiated by Sellnick (1944, 1958) specifically for mites of the family Zerconidae. All three systems are now in use by various authors who continue to describe taxa of Zerconidae. Although the two modified systems are discordant in their notations for setae of the podonotal region, they are largely accordant for setae of the opisthonotal region. Sellnick applied his system primarily to the opisthonotal shield of adult zeronid mites, though he outlined it for the podonotal shield, without notation, in his 1944 paper and with notation in his 1958 paper. His system recognized four longitudinal series of setae: an “Innenreihe” or dorsocentral row, i-I (also denoted alternatively by him and some other authors as j-J to avoid confusion when used with numerals), a “Zwischenreihe” or mediolateral row, z-Z, a “Seitenreihe” or lateral row, s-S, and a “Randreihe” or marginal row, r-R. For the holotrichous condition on the podonotum of zeronid mites, Sellnick designated six pairs of setae, i1-i6 (or j1-j6), in the dorsocentral series, two pairs, z1-z2, in the mediolateral series, six pairs each, s1-s6 and r1-r6, in the lateral and marginal series, respectively, plus two or three pairs, p1-p3, designated as “peritrematal” setae, for a total of 22 or 23 pairs of setae. For the holotrichous condition on the opisthonotum of zeronid mites, he designated six pairs of setae, J1-J6 (or J1-J6), in the dorsocentral series, five pairs, Z1-Z5, in the mediolateral series, four pairs, S1-S4, in the lateral series, and usually seven or eight pairs, R1-R8, in the marginal series, for a total of 22 or 23 pairs of setae. Sellnick did not consider whether the opisthonotal setae could be arranged in transverse ranks, which might reflect vestiges of metamerism; therefore, he was not concerned about the different numbers of setae in each row. However, transverse ranks were considered subsequently by Hirschmann (1957, 1959) for the opisthonotal region, and by Lindquist & Evans (1965) for both the podonotal and opisthonotal regions, when they applied their modifications of Sellnick’s system to a wide array of other families of free-living Gamasina. For the opisthonotal region, basically five setal pairs were recognized by these authors for each of the J, Z, S series. Additional setae were interpreted as “extra” designatable idionymic setae or, if variably numerous and asymmetrical, then as non-designatable, adelonymic setae sensu van der Hammen (1975).

The great majority of specialists who have described species of zeronid mites (e.g., Halašková, 1963, 1969 and other papers, Aoki, 1964, and other papers, Blaszak, 1974, and many other papers, Kosir, 1974, Mihelčič, 1963, and other papers, Petrova, 1977a, and other papers, Balan, 1991, and other papers) have opted to follow Sellnick (1944, 1958) in recognizing generally 6 pairs of J-setae and 4 pairs of S-setae on the opisthonotum. However, Athias-Henriot (1961) and Karg (1965, 1993) followed Hirschmann (1957), while Moraza (1988 and other papers) and Johnston & Moraza (1991) followed
Lindquist & Evans (1965), in recognizing generally 5 pairs each of \( J \)- and \( S \)-setae. In doing so, these authors consistently admitted an “extra” pair of setae, denoted \( Zx \) by Hirschmann (1957, 1959) and \( Jx \) (or \( Jx \)) by Karg (1965, 1993), between setae \( J3 \) and \( J4 \), and they denoted the first pair of setae in a marginal position as \( SI \), rather than \( RI \). The “extra” pair of setae was recognized as a diagnostic apomorphy of Zerconidae by Karg (1965, 1993).

As noted by Lindquist (1994), 6 setal pairs in the opisthonotal \( J (=1) \) series is an exceptional holotrichous number, whether interpreted as \( JJ-J6 \) or as \( JJ-J5 \) plus a pair \( Jx \). This condition is all the more anomalous, as the “extra” pair was found in this study to be present beginning with the protonymphal instar; yet the protonymph has the normal holotrichous number, 15 pairs, of opisthonotal setae characteristic of various families of the mesostigmatic cohort Gamasina. This anomaly has prompted us to review the ontogeny and homology of the idiosomal setae among various taxa of zerconid mites, in order to confirm whether the holotrichous condition in Zerconidae is like that in other families of Gamasina. On that basis, the additional objectives of this paper are to determine whether the notation applied to these setae in Zerconidae needs re-interpretation, and to present a standardized notation that will facilitate accurate homology and designation of idiosomal setae among the variety of taxa in this family.

**Material and methods**

This study is based in part on our examination of complete (larva, protonymph, deutonymph, adult) or partial (protonymph linked with adult) ontogenetic series of conspecific, slide-mounted specimens of several species of Zercon, Parazercon, Prozercon and Skeironozeron at hand in the Canadian National Collection of Insects and Arachnids, Agriculture and Agri-Food Canada, Ottawa, and the Museum of Zoology, University of Navarra, Pamplona. It is also based on our examination of annotated illustrations accompanying descriptions of similarly complete or incomplete ontogenetic series of nearly 30 species in 6 genera of Zerconidae that are available in the literature, including 6 species of Prozercon (Halašková, 1963, 1969, Blaszk, 1974, 1979, Urhan & Ayyildiz, 1996), 1 of Parazercon (Halašková, 1969, Blaszk, 1974, 1979), 1 each of Caurozercon and Skeironozeron (Halašková, 1977), 1 of Mixozeron (Blaszk, 1974), and 19 of Zercon (Halašková, 1969, 1977, Blaszk, 1974, 1979, Moraza, 1991).

The number, position and ontogenetic expression of idiosomal setae of these taxa were compared with the general pattern found among representatives of a wide variety of other families of free-living, holotrichous gamasine mites that have been studied and illustrated by Hirschmann (1957), Karg (1962, 1965) and Lindquist & Evans (1965) or that have been studied by us. Our decisions made in revision of homologies of certain idiosomal setae are based on comparisons of these patterns and on the rationale of morphological parsimony to account for apparent differences in patterns. Finally, we tested the consistency of our revised notation by applying it to illustrations of adult idiosomal setation that are available in the literature for all 40 genus-group taxa of Zerconidae (Table 4).

Morphological observations of mites mounted in Hoyer’s medium on microslides were made using compound microscopes equipped with differential interference contrast and phase-contrast optical systems. Idiosomal setal notation generally follows the system of Lindquist & Evans (1965), with modifications for the posterior region as given by Lindquist (1994). Notational equivalents of this system with those of Hirschmann (1957) and Sellnick (1944, 1958) are given in Tables 1–3. Distinctions between porelike structures of the idiosoma as either gland pores (solenostomes) or poroids (lyrifissures) are based on the morphological observations of Athias-Henriot (1969a, 1969b) and subsequent physiological findings of Krantz & Redmond (1987). Notation for these structures, as adenotaxy and poroidotaxy, respectively, follows that of Johnston & Moraza (1991); using this notation, the prominent two pairs of opisthonotal gland pores \( gdZ3 \) and \( gdZ4 \) are homologous with those denoted as \( Po3 \) and \( Po4 \) by authors for zerconid mites.
TABLE 1: Ontogeny and notational equivalents for podonotal setae in Zerconidae. First column of sigla follows LINDQUIST & EVANS (1965); second column follows HIRSCHMANN (1957) and subsequent papers by KARG; third column follows many papers of HALASKOVÁ, BLASZAK and subsequent authors; fourth column follows SELLNICK (1944, 1958). Abbreviations: lv, larva; pn, protonymph; dn, deutonymph. Disparate usages within one notational system indicated by two sigla in one position. Parenthetical siglum indicates setal homologue of gamasine mites that is absent in Zerconidae.

**Observations and Results**

**Ontogeny of Podonotal Setae. Larva.** The idiosoma of holotrichous larval gamasine mites generally has 10 pairs of podonotal setae, of which 9 pairs (j1, j3-j6, z2, z4, z5, s4) are usually on a large podonotal shield and one pair (s6) on soft cuticle behind the posterolateral corners of this shield (Fig. 1). The larvae of a variety of zerconid mites (species of Zercon, Prozercon, Parazercon, Mixozzercon) have the same complement of setae in the same position as in other families of Gamasina and, therefore, the homologies of these setae are confirmed (Fig. 2).

**Table 2:** Ontogeny and notational equivalents for opisthonotal setae in Zerconidae. See Table 1 for explanation of author subheadings, abbreviations, and double entries.

**Table 3:** Ontogeny and notational equivalents for opisthogastric setae in Zerconidae. See Table 1 for explanation of author subheadings, abbreviations, and double entries. Sellnick’s system was not applicable to ventral setae. Parenthetical siglum follows modified notation of LINDQUIST (1994).
Protonymph. Five or six pairs of podonotal setae ($j_2$, $s_5$, $r_2$, $r_3$, $r_5$, sometimes $s_6$) are generally added to the larval complement in the protonymph of holotrichous Gamasina, which then has 15 or 16 pairs of podonotal setae (Fig. 5). Protonymphs retain a separate podonotal shield, but the breadth of this shield varies among families, such that the marginal setae may be off this shield or, as in the case of zeroncid mites, on it (Fig. 6). The same complement of setae is added in the same relative positions in zeroncids as in other holotrichous gamasine mites, so again we can confirm the homologies of these setae. Setae $r_2$ or $r_3$ are not shown in figures by some authors for protonymphs of some species of Zeroncidae. As these setae are inserted on the edges of the podonotal shield, which may be curved ventrolaterally, they may have

Figs. 1-2: Idiosomal dorsum of larval Gamasina.

been overlooked. The “humeral” pair of setae, r3, is in a somewhat more ventrolateral than dorsolateral position in zerconid protonymphs than in most other Gamasina, but its ontogenetic expression and position between setae r2 and r5 is otherwise typical.

Deutonymph and Adult. The number of podonotal setae on the deutonymph increases to the adult complement in holotrichous gamasine mites, with setae z1 (when present), z3, z6 (if not already added), s1-s3, r1 (when present), r4, r6 (when present) being added to the previous protonymphal complement. The deutonymph then generally has 21 to 23 pairs of podonotal setae. The deutonymphal podonotal shield remains separate in some families of Gamasina, including Zerconidae (Fig. 10), but it is partly or completely fused to the opisthonotal shield in others (Fig. 9). Again, the same complement of setae is added in the same relative positions in zerconid mites as in other holotrichous Gamasina, such that we can confirm the homologies of these setae as designated herein. Holotrichous zerconid mites generally have 21 to 23 pairs of podonotal setae, with only setae r6 of the general chaetome of Gamasina consistently absent.

Setae z1 are absent in many taxa of Zerconidae, including all members of the speciose genus Zercon.
Koch and of 27 of the 35 other genera described (Table 4). When present, z1 are generally small and inserted closely beside setae j1-j2 on the anterolateral margins of the podonotal shield (Figs. 17B, 19A, 24). These margins may be curved ventrally, like a shell, in adults of some genera (e.g., Parazercon Trägårdh, Parazozercon Blaszak, Kalkiozercon Halašková, Skeironozercon Halašková). In these cases, setae z1 are tiny and somewhat ventrally displaced (Fig. 17B), and they have been considered to be an anteriormost pair of either “peritrematal” or lateral setae. Accordingly, with Sellnick’s system, they have been denoted either as px for Parazozercon and Parazozercon (Blaszak 1979, 1981a), or as xl for Parazozercon and Skeironozercon (Halašková, 1977; Blaszak, 1982), or left undenoted in the case of Kalkiozercon mamillo­sus (Halašková, 1979), with resultant uncertain homology. Setae z1 were not noted in descriptions by Petrova (1977b) and Halašková (1979) for some species of Parazozercon and Skeironozercon, but they may have been overlooked. Setae z1 are more exposed and obvious in Aspar Halašková (Fig. 24), in which they were denoted as xl (Halašková, 1977). In members of the genus Echinozercon Blaszak, setae z1 (denoted as xl by Blaszak, 1976, 1982) are unusual in being moderately long and located in a position similar to setae z2 in other genera of Zerconidae (setae z2 and z3 are in turn displaced further posterolaterally in this genus) (Fig. 19A). Based on their position, setae denotable as z1 are apparently present, closely lateral setae j1, in the monotypic genera Syskenozercon Athias-Henriot and Halazozercon Wiśniewski et al. (the latter genus was transferred from Halolaelapidae to Zerconidae by Moraza & Lindquist, in press). Except for the vertex, on which these two pairs of setae are inserted, the idiosomal dorsum of adults of these genera is strongly neotrichous, such that the homologies of other dorsal setae are obscure.

Application of Hirschmann’s system has not been clear for the pair of setae denoted by us as z1 for Zerconidae. In their illustrated notation for Zerconi­dae, both Hirschmann (1957, 1983) and Karg (1971, 1993) accounted for only 21 of the 23 pairs of podonotal setae known to occur among members of this family. Of the two pairs not accounted for, one is clearly z1, and the other is probably z3 (only one seta, denoted by them as s2, was shown in the area usually occupied by the highly stable, ontogenetically larval setae z2 and the less stable, ontogenetically deutonymphal setae z3). Hirschmann (1983) alluded to an “extra” pair, rz, in the rhodacarid genus Rhodacarus which has 23 pairs of podonotal setae, but this was not noted for Zerconidae.

Setae r1 are generally short, erect, and positioned laterad or ventrolaterad setae z3. They are inserted either on the peritrematal shields (Figs. 17B, 20B), or in the area of confluence of these shields with the podonotal shield (Figs. 14, 22), in adults of all known members of Zerconidae except the monotypic genus Monozercon Blaszak. Adults of this genus are unique, according to Blaszak (1984), in lacking r1, and they also lack setae z1, z3 and s2 along the anterolateral margins of the podonotal shield (Table 4). Because of their location, setae r1 have been consistently denoted as “peritrematal” setae pl by various authors who have used Sellnick’s system of notation. They have been denoted as r2 by authors following Hirschmann’s system, though Karg (1993) did not denote this pair of setae in any of his figures of Zerconidae.

Setae r2 are inserted on the peritrematal shields of adults in a few genera (e.g., Aspar Halašková, Parazercon Trägårdh, Parazozercon Blaszak, Skeironozercon Halašková) (Figs. 17B, 24), but on the edge of the podonotal shield of those in others (Figs. 14, 18A, 22). As “peritrematal” setae, they were denoted as p3 by Sellnick (1958), followed by Blaszak (1976), but as p2 by Halašková (1977). As marginal setae, the same pair was denoted as r2 by Sellnick (1958), followed by Kosir (1974), but as r3 by Halašková (1963, other papers), Blaszak (1974, other papers) and Petrova (1977b, 1978). All of these authors were using Sellnick’s system of notation, but they were implying four different homologies for the same pair of setae (Table 1). Marginal setae r2-r5 are consistently present in deutonymphs and adults of Zerconidae, but their size and position with respect to the peritrematal shields varies considerably among taxa; it is important to account for and denote them before accounting for some of the adjacent setae. Setae r2 are close to r3, but, as just noted, they may not be inserted as ventrolaterally as r3, and instead may be aligned marginally with setae s2.

The position of setae z2, an ontogenetically stable pair that is present in all known taxa of Zerconidae, is
### Table 4: Dorsal idiosomal setae and miscellaneous attributes of genera (and subgenera) of *Zerconidae.*

Infrequent numbers of setae indicated in boldface; ± indicates presence or absence. "Oddities" of opisthonotal setae indicate distinctive character states of some genera; "duplex R's" refers to individually duplicate marginal setae. Abbreviations and word meanings under column, Miscellaneous Attributes: fused d.sh., podonotal and opisthonotal shields united; jugularia, separate sternal platelets with sternal setae and poroids I; longer perit., peritremes extending at least to midlevel of coxae II; shell, podonotal shield carapace-like, extended anteroventrally and lateroventrally; wee perit., peritremes abbreviated, not reaching beyond posterior margin of coxae III; r2=p3, setae r2 inserted so as to appear like 3rd pair of peritrematal setae. See text for further explanation.

<table>
<thead>
<tr>
<th>Genus Name</th>
<th>Podonotal Setae</th>
<th>Opisthonotal Setae</th>
<th>Misc. Attributes</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Alekszercon</em> Petrova 1978</td>
<td>22 zl</td>
<td></td>
<td>shell, fused d.sh.</td>
</tr>
<tr>
<td><em>Allozercon</em> Blaszak 1984</td>
<td>22 zl</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Amerosercon</em> Halaskova 1969</td>
<td>22 zl</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Aquulonosercon</em> Halaskova 1979</td>
<td>22 zl</td>
<td>J5-Z4 aligned</td>
<td>shell</td>
</tr>
<tr>
<td><em>Aspar</em> Halaskova 1977</td>
<td>23</td>
<td>J4-Z3-Z4 aligned</td>
<td>shell, r2=p3</td>
</tr>
<tr>
<td><em>Bakeras</em> Blaszak 1984</td>
<td>22 zl</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Bledas</em> Halaskova 1977</td>
<td>22 zl</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Carpathosercon</em> Balan 1991</td>
<td>22 zl</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Cauzercon</em> Halaskova 1977</td>
<td>22 zl</td>
<td>duplex R's</td>
<td>shell</td>
</tr>
<tr>
<td><em>Cosmazercon</em> Blaszak 1981a</td>
<td>22 zl</td>
<td>± J2, J4 duplex R's</td>
<td>longer perit.</td>
</tr>
<tr>
<td><em>Echinozercon</em> Blaszak 1976a</td>
<td>23</td>
<td>± J2, J4 duplex R's</td>
<td>longer perit.</td>
</tr>
<tr>
<td><em>Eurozercon</em> Halaskova 1979</td>
<td>22 zl</td>
<td></td>
<td>shell</td>
</tr>
<tr>
<td><em>Halacecon</em> Wiśniewski et al. 1992</td>
<td>&gt;60</td>
<td></td>
<td>neotrichy</td>
</tr>
<tr>
<td><em>Hypazercon</em> Blaszak 1981b</td>
<td>22 zl</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Indozercon</em> Blaszak 1978</td>
<td>22 zl</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Kalkizercon</em> Halaskova 1979</td>
<td>22-23 ± zl?</td>
<td>± J5</td>
<td>shell</td>
</tr>
<tr>
<td><em>Koreazercon</em> Halaskova 1979</td>
<td>22 zl</td>
<td></td>
<td>shell</td>
</tr>
<tr>
<td><em>Krantisaz</em> Blaszak 1981b</td>
<td>22 zl</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Lindquistaz</em> Blaszak 1981b</td>
<td>22 zl</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Macroazercon</em> Blaszak 1976a</td>
<td>22 zl</td>
<td></td>
<td></td>
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<tr>
<td><em>Metazercon</em> Blaszak 1976a</td>
<td>22 zl</td>
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<tr>
<td><em>Metazercon</em> Blaszak 1976a</td>
<td>22 zl</td>
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<tr>
<td><em>Microazercon</em> Blaszak 1976a</td>
<td>22 zl</td>
<td></td>
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<tr>
<td><em>Mixaz</em> Halaskova 1963</td>
<td>22 zl</td>
<td></td>
<td></td>
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<tr>
<td><em>Monoazercon</em> Blaszak 1984</td>
<td>19 z1, z2, z3, z4</td>
<td>Z2</td>
<td>wee perit.</td>
</tr>
<tr>
<td><em>Nezercon</em> Petrova 1977b</td>
<td>22 zl</td>
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<td></td>
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<tr>
<td><em>Paleazercon</em> Blaszak et al. 1995 [fossil]</td>
<td>22 zl</td>
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<tr>
<td><em>Parazercon</em> Tragardh 1943</td>
<td>22-23 ± z6</td>
<td>± J5</td>
<td>shell, r2=p3</td>
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<tr>
<td><em>Perhazercon</em> Blaszak 1981a</td>
<td>23</td>
<td>J5</td>
<td>shell, r2=p3</td>
</tr>
<tr>
<td><em>Polazercon</em> Blaszak 1979</td>
<td>22 zl</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Proazercon</em> Sellnick 1943</td>
<td>22 zl</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Przercon (Plumatazercon)</em> Balan 1992</td>
<td>22 zl</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Rafar</em> Blaszak 1979</td>
<td>22 zl</td>
<td></td>
<td>jugularia</td>
</tr>
<tr>
<td><em>Skeironazercon</em> Halaskova 1977</td>
<td>23</td>
<td>J2</td>
<td>wee perit., r2=p3</td>
</tr>
<tr>
<td><em>Syskenazercon</em> Athias-Henriot 1976</td>
<td>&gt;50</td>
<td></td>
<td>neotrichy</td>
</tr>
<tr>
<td><em>Xenazercon</em> Blaszak 1976b</td>
<td>22 zl</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Zzercon (Zerconella)</em> Willmann 1953</td>
<td>22 zl</td>
<td>J5</td>
<td></td>
</tr>
<tr>
<td><em>Zzercon (Iszercon)</em> Blaszak 1979</td>
<td>22 zl, ± z3</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Zzercon (Iszercon)</em> Karag 1993</td>
<td>22 zl</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Zzercon</em> Koch 1841</td>
<td>21-22 z1, ± z1</td>
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</tr>
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</table>
also important to determine before accounting for some adjacent setae. In larvae and protonymphs of Zerconidae, as in other families of Gamasina, this is the first pair of setae encountered posterolaterad gland pores gdj2 (Fig. 6). That position is maintained in zerconid deutonymphs and adults, in which z2 are often inserted marginally, laterad oblique alignment between gland pores gdj2 (prominent structures, denoted as pores pol in papers by HALAŠKOVÁ and BLASZAK) and poroids idj3 (Figs. 10, 14, 18A). Setae z2 are denoted as s2 in the systems of both SELLNICK and HIRSCHMANN (Table 1); however, they were deno-
ted as $s1$ by BŁASZAK (1976), using SELLNICK's system in description of *Echinozercon orientalis* Błaszak. Setae $z3$ are next in line posterolaterad $z2$, where they are nearly transversely aligned with $rl$ (Figs. 14, 22). Sometimes they are fully marginal in position, and lie just above $rl$, when the lateral margins of the podonotal shield are curved ventrally, somewhat like a shell (Figs. 17B, 18A, 20A). Authors using either of the systems of SELLNICK or HIRSCHMANN for zeronid mites generally have denoted these setae as $s3$. In many genera of Zeronidae, however, $z3$ are larger and more marginal and erect in appearance than $z2$ (Fig. 18A), and they have been denoted as $rl$, instead of $s3$, by some of the same authors using the same
notational system of Sellnick (e.g., Halášková, 1963 and other papers, Blaszak, 1974, 1981b and other papers); such notational inconsistencies have obscured the homology of this pair of setae (Table 1).

Setae $z_4$ constitute another ontogenetically stable pair that is present in all known taxa of Zerconidae; their position, like that of $z_2$, is also important to determine before accounting for some other adjacent setae. In larvae and protonymphs of Zerconidae, as in other families of Gamasina, these setae are located laterad gland pores $gd_{j4}$ (Fig. 6). That position is maintained in zerconid deutonymphs and adults, in which gland pores $gd_{j4}$ are often prominent structures (denoted as pores $po_2$ in papers by Halášková and Blaszak) (Figs. 10, 14, 18A). The pair of setae denoted by us as $z_4$ should be denoted as $s_4$ by authors using Sellnick’s system of notation. But, whenever the preceding pair $z_3$ have been denoted by some of these authors as $r_1$ instead of $s_3$, as noted above, then in turn pair $z_4$ has been denoted as $s_3$ instead of $s_4$, again obscuring setal homologies (Table 1). A similar, “domino effect” discrepancy in notation has occurred for the lateral setae that we denote as $s_4$ and $s_5$. These setae should be denoted as $s_5$ and $s_6$, respectively, by the various authors who have followed the systems of Sellnick or Hirschmann. However, Blaszak (1974, 1981b and other papers) denoted these pairs as $s_4$ and $s_5$, respectively, in genera such as Prozercon and Krantzaz, but as $s_5$ and $s_6$ in others such as Parazercon and Zercon. Among the same authors who have used Sellnick’s system, the “domino effect” discrepancy has followed with other of the lateral $s$- and marginal $r$-setae, depending on how many of these are in a marginal position, such that our $s_3$ has been denoted as either $r_3$ or $r_4$, our $r_4$ as $r_4$ or $r_5$, our $r_5$ as $r_5$ or $r_6$, and our $s_6$ as $r_6$ or $r_7$ (Table 1). The Sellnick system of notation itself should not be blamed for these incon-
ONTOGENY OF OPISTHONOTAL SETAE. Larva. The idiosoma of holotrichous larval gamasine mites generally has 10 pairs of opisthonotal setae (J2-J5, Z3-Z5, S3-S5), a variable number of which may be on a pygidial shield, depending on its size. Fig. 1 shows a typical configuration of these setae relative to the pygidial shield in the Ascidae. According to our observations and those of KARG (1962, 1965), in some families (e.g., Veigaiidae, some Phytoseiidae) some of these setae are vestigial or absent and the pygidial shield is absent. Due to the posteroventral curvature, or “caudal bend” of the opisthosoma (SITNIKOVA, 1978; LINDQUIST, 1984), the caudalmost pair of each of the J, Z and S series is located caudoventrally, with Z5 and S5 on soft cuticle flanking the circumanal setae and J5 on the posterior margin of the pygidial shield (when present), just behind the circumanal setae (Fig. 3). The larvae of a variety of zerconid mites have the same complement of setae in the same
position as in those of other Gamasina, though the pygidial shield is sufficiently expanded laterally so as to capture setae S4 (denoted as S3 by Karg, 1965), and in a few cases anteriorly, so as to capture setae J3 and even J2 (e.g., Prozercon kochi Sellnick as illustrated by Blaszak, 1974). Thus, the homologies of these setae on larvae of Zerconidae are readily compared and confirmed with those on larvae of other holotrichous families of Gamasina (Figs. 1-4).

As noted below, setae J2 are absent in postlarval instars of a few taxa of Zerconidae, including Skeironozcon embersoni Halasková and Echinazercon orientalis Blaszak. Setae J4 are also absent in E. orientalis. Although larvae are not yet known for these taxa, the losses are probably larval setal deficiencies, as these setae, when present, are usually part of the larval complement. Setae J5 are absent in postlarval instars of Parazercon radiatus (Berlese).

These setae are also elements of the normal larval complement, and we have confirmed their absence in the larva of this species. Setae J5 are also apparently absent in Zercon (Zerconella) leitnerae Sellnick, according to the description and illustration of Sellnick (1958).

Protonymph. Five pairs of opisthonotal setae (J1, Z1, Z2, S2, R1) are generally added to the larval complement in protonymphs of holotrichous Gamasina, which then have 15 pairs of opisthonotal setae (Fig. 5). A variable number of these setae may be on the pygidial shield which, if present, is more variable in size than in the larva. The relative size of this shield and the number of setae borne on it were used as diagnostic attributes in the superfamilial classification of Karg (1965, 1993). The pygidial shield of protonymphs remains separate from the podonotal shield, but it may be expanded enough to coalesce.
with some or all of the mesonotal platelets and thus be more appropriately termed an opisthonotal shield. As noted by KARG (1965), protonymphs of Zerconidae are extreme in the direction of enlargement of the pygidial shield, such that it assumes the form of an opisthonotal shield and bears 14 to 16 pairs of setae, including J2-J5, Z1-Z5, S2-S5, and sometimes J1 and the single pair of marginal setae present, RI (Fig. 6). Apart from the size of the opisthonotal shield, the same complement of setae is added in the same relative positions in zeronid mites as in other holotrichous gamasine mites, enabling us to confirm the homologies of these setae readily, except for either one of two pairs of setae identifiable as an apparent 16th pair of opisthonotal setae. One of the pairs in question was denoted as Zx by HIRSCHMANN (1957, 1959, 1983), and as Jx (or Jx) by KARG (1965, 1993), despite the fact that this pair was originally designated as J4 by SELLNICK (1944, 1958) when he initiated his system of notation for Zerconidae (Table 2). The other pair in question was designated as J5 by SELLNICK (1944, 1958), but recognition of a “J6” appeared anomalous to HIRSCHMANN (1957) and KARG (1965), who recognized 5 pairs of setae in each of the J, Z and S series in holotrichous gamasine mites. They opted to denote this pair as J5 (or J5), and to recognize instead an “extra” pair between the setae that they denoted as J3 and J4 on zeronid mites.

We question the accuracy of the designation Jx (or its equivalent Jx or Zx), or of any alternative recognition of six pairs of J-setae (e.g., designation of J1-J6 by SELLNICK, 1944, 1958), for three reasons. First, among mites of all other families of free-living, holotrichous gamasine mites with which we are familiar, a single pair of extra or accessory setae does not appear during ontogeny at the protonymphal stage; i.e., only ontogenetically fundamental setae are present. Second, if one accounts for all opisthosomal setae...
present both dorsally and ventrally, then zerconid protonymphs have the same number that is present in holotrichous protonymphs of other families—20 pairs, excluding the genital pair st5, the euanal pair and the unpaired postanal seta (Figs. 5-8). Third, based on the previous two points, it is highly improbable that one of the relatively stable pairs of setae, which is typical of gamasine protonymphs and is amidst a series of setae already present in the larval instar, would be suppressed as a postlarval deficiency (sensu Lindquist, 1965), and that another pair of setae, which is not typical of gamasine protonymphs, would abruptly appear in the protonymphal stage in Zerconidae. Such an alternative is neither logical nor morphologically parsimonious. Therefore, an accounting for the opisthosomal setae on the ventral surface may lead to a re-evaluation of the homologies of setae on the dorsal surface.

As noted by Karg (1965), Lindquist & Evans (1965) and other authors, the number of opisthogastric setae, apart from the genital pair st5, does not increase from the holotrichous larva to the holotrichous protonymph among the families of Gamasina. However, the caudal bend of the larva disappears in the protonymph, such that setae J5, Z5, S5 assume a dorsocaudal, instead of a ventrocaudal, position and setae JV5 assume a ventrocaudal position in place of where Z5 are inserted in the larva (compare Figs. 3 and 7, 4 and 8). Zerconid protonymphs are as distinctive in the extent of their opisthogastric shielding as they are of their opisthontal shielding. As a result, all but one pair (JVJ) of the 6 pairs of opisthogastric setae are on a ventrianal shield. Equally notable and unusual, this ventrianal shield is broadly coalesced
caudally with the opisthonotal shield, such that delineation of the posterior margins of these shields is effaced (Figs. 6, 8). Setae JV5 occupy a nearly marginal position posterolaterad gland pores gv3 and poroids ip (Fig. 8). Setae JV5 are thus in a somewhat more caudal position in protonymphs of Zerconidae than in those of most other Gamasina, but their ontogenetic expression and position relative to adjacent setae are otherwise typical.

In view of the above characteristics in number, position and ontogeny of opisthosomal setae among the larvae and protonymphs of Zerconidae, the homologies of these setae are clear and their sigla are modified as follows (Table 2). The pair of J-setae previously denoted by HIRSCHMANN (1957) and KARG (1965) as “extra” Zx or Jx is J4, and the pair previously denoted by them as J4 is J5, as originally recognized by SELLNICK (1944, 1958). However, there is no need to recognize an anomalous sixth pair of J-setae, as the pair denoted J6 by Sellnick is actually Z5. In turn, the other pair of setae on the caudolateral margin, denoted Z5 by Sellnick and subsequent authors, is JV5. The homologies and sigla of all other opisthonotal setae (J1-J3, Z1-Z4, S2-S5, R1) and opisthogastric setae (JV1, JV2, ZV2) are the same as designated previously, and the entire normal, holotrichous setation of the protonymphal opisthosoma of the Gamasina is thus present and accounted for. Zerconid mites are remarkably conservative in retaining a holotrichous condition on the opisthonotum, though as noted above for the larvae, one or two pairs of setae in the J-series may be absent from the protonymphal complement of a few taxa, and these losses persist in their deutonymphs and adults.

Deutonymph and Adult. As with the podosoma, the number of setae on the deutonymphal opisthosoma increases to the adult complement in holotrichous gamasine mites (Figs. 9, 10). Setae SI, R2-R7 and, if present, a variable number of submarginal (UR) setae are added dorsally and laterally, and setae JV3, JV4, ZV1, ZV3, ZV4 and, if present, ZV5, SV2 are added ventrally to the previous larval-protonymphal com-

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Fig. 18: Idiosomal dorsum, A, and idiosomal venter, B, of adult female Prozercon juanensis Moraza, showing variation in position of setae between genera of Zerconidae (compare with Figs. 14, 17, 19, 20, 22, 24) (redrawn and modified from Moraza, 1988).
Deutonymphal dorsal and ventral shielding varies greatly among families of Gamasina. Dorsally, there is usually a well developed opisthonomatal shield, which may be separate from or united to the podonotal shield; the opisthonomatal shield is usually less expansive laterally than in adults, such that the R-marginal series of setae usually remains on soft cuticle flanking it. Ventrally, there is either an anal or an expanded ventrianal shield, which is usually separate caudally from the opisthonomatal shield. As in the case of their protonymphs, the deutonymphs of Zerconidae are extreme in the extent of enlargement of their opisthosomal shields. The opisthonomatal shield bears all 21 or 22 pairs of holotrichous dorsal setae present, including $J_1$-$J_5$, $Z_1$-$Z_5$, $S_1$-$S_5$, and 6 or 7 pairs of $R$-setae; it also superficially bears the somewhat dorsocaudally displaced ventral pair, $JV_5$, as in the protonymph (Fig. 10). Careful observations show, however, that the insertions of setae $JV_5$ generally remain slightly more caudal and ventral than those of the neighboring setae $Z_5$, $S_5$, and $R_6$ or $R_7$. Although the ventrianal shield in zerconid deutonymphs is not so expansive as to capture the metapodal plates as in adults, it nevertheless captures all opisthogastic setae present, other than $JV_5$. In the holotrichous condition, these include $JV_1$-$JV_4$, $ZV_1$-$ZV_4$, and the circumanal setae (Fig. 12, Table 3) (setae $ZV_5$ appear

Fig. 19: Idiosomal dorsum, A, and peritrematal shield, B, of adult female Echinozercon orientalis Blaszak, showing variation in position of setae between genera of Zerconidae and duplication of opisthonomatal marginal setae (compare with Figs. 14, 17, 18, 20, 22, 24) (redrawn and modified from Blaszak, 1976).
to be consistently absent in Zerconidae, unless they may be represented by the caudalmost pair of setae in a marginal position, which are denoted as $R7$ herein). Apart from the sizes of the opisthosomal shields, the same complement of setae is added in the same relative positions in deutonymphs of Zerconidae as in those of other holotrichous Gamasina. This pattern enables us to confirm the homologies of these setae in deutonymphs and adults, as we have done with protonymphs, of this family with those of other Gamasina (Figs. 9-16).

The anomaly of having only 4 pairs of setae in the $S$-series, in contrast to 5 or 6 pairs in the $Z$- and $J$-series as originally designated by SELLNICK (1944, 1958) for zeronid mites, was resolved by HIRSCHMANN (1957) and KARG (1965), and confirmed by LINDQUIST & EVANS (1965). The anteriormost pair of the $S$-series is often in a more marginal position than other setae of this series in gamasine mites (HIRSCHMANN 1957, and our personal observations). In Zerconidae, pair $S1$ is aligned with the marginal series and it was mistaken as $R1$ by SELLNICK. This mistaken designation has been followed subsequently by most specialists working on Zerconidae (e.g., BLASZAK, HALASKOVÁ, PETROVA, KOSIR, BALAN—see references noted above). In turn, in some cases (e.g., species of Parazercon, Mixozercon) setal pair $S2$ is nearly aligned with, and may be mistaken for, an element of the mediolateral or $Z$-series. In such cases, $S2$ is the second seta in alignment, between $Z1$ and $Z2$ (Figs. 17A, 19A, 22, 24).

The positions of setae of the $Z$- and $S$- series vary

remarkably among adults of some taxa of Zerconidae. In some species of Echinozercon and Caurozercon, setae Z1-Z4 are completely aligned and interdigitated longitudinally with S2-S4, and their sequence is Z1-S2-Z2-S3-Z3-S4-Z4 (Figs. 19A, 22). In Mesozercon, setae Z1-Z4 are crowded together in the anterior region of the opisthonotal shield, where they are widely separated from Z5 (Fig. 20A); however, just which setal pair is Z4, in distinction to S3 or S4, is problematical based on adults and deutonymphs of this genus. In Aspar, setae Z3-Z4 are displaced posteriorly, in longitudinal alignment between J4 and J5 (Fig. 24). The homologies of the setae involved in such cases may be clarified by study of the protonymph and, sometimes, the deutonymph of the same species, or of adults of other species of the same genus in which the setal displacements are less extreme (compare Figs. 21 with 22, and 23 with 24).

DISCUSSION

Re-evaluation of idiosomal setal homologies and their notation based on the above findings offers some new perspectives on characteristics that are diagnostic for the Zerconidae as well as for the superfamily Zerconoidea, which includes Zerconidae and Coprozerconidae (Moraza & Lindquist, in press). Instead of holotrichous members of this superfamily being characterized by having an extra pair of J-setae, the normally caudoventral opisthogastrial setae JV5 are displaced to a somewhat caudodorsal position so as to appear to be captured by the opisthonotal shield—an autapomorphy peculiar to this group. Other apomorphic attributes are correlated with this setal displacement in the Zerconidae in distinction to Coprozerconidae, i.e., the coalescence...
of the posterior margins of the opisthonotal and opisthogastric shields, and the somewhat anterior displacement and crowding of the posterior setae of the J-series, J5, such that they are usually nearly transversely aligned with setae Z4 rather than being located well behind the latter. As setae Z5 are inserted along with JV5 on the caudal margin of the opisthosoma, both pairs often are included by authors in their figures of the ventrianal shield of adults, and Z5 may be mistaken for a pair of opisthogastric setae unless they are correctly designated otherwise.

The revised homologies of opisthosomal setae for Zerconidae also are in accord with neighboring pore-like structures and dorsoventral muscle attachment sites (sigilla), which together with setae may be used to delimit “organogerous areas” (“territoires organogènes”) sensu ATHIAS-HENRIOT (1975). For example, in Zerconidae, the setal pair re-designated J4 is in approximate oblique alignment with poroids idZ3 (idm4 of ATHIAS-HENRIOT) and the fourth opisthonaotal sigilla (sa XII of ATHIAS-HENRIOT); these structures constitute elements of the fourth paraxial, opisthonotal, organogerous area (C12 of ATHIAS-HENRIOT), as in other families of Gamasina. As another example, the positions of the two prominent pairs of gland pores, gdZ3 near setae Z3, and gdZ5 near setae S5, in Zerconidae also are in accord with the positions of these pores (denoted gd8 and gd9 by ATHIAS-HENRIOT, 1975) in other families of Gamasina where they are less prominent. These two sets of pores and setae can be seen in Zerconidae to be elements of the same two organogerous areas, denoted M6 and L7 by ATHIAS-HENRIOT (1975), as delineated by her for other families of Gamasina.

Setae J5 of zeronid mites are usually situated just anterior to the transverse row of four, often sclerotized, fossae situated near the posterior margin on the opisthonotal shield. This location may appear to be discordant with their position behind the transverse row of four sigilla (the fifth set of opisthonotal sigilla, denoted sa XIV by ATHIAS-HENRIOT, 1975) that are near the posterior margin on the opisthonotal shield in other families of Gamasina. However, as noted by ATHIAS-HENRIOT (1970), dorsoventral idiosomal sigilla undergo a high degree of functional adjustment, such that there is considerable variation in their patterns among different families of Gamasina. Even in some Zerconidae, setae J5 remain inserted slightly behind the row of fossae, as illustrated by PETROVA (1979) and confirmed by our observations for species of Caurozercon. Moreover, according to EVANS (1992), the inner surfaces of these fossae may be sites of additional dorsoventral muscles in Zerconidae, rather than sites of the fifth basic set of dorsoventral opisthosomal muscles normally associated with the posterior row of sigilla in other families.

Setal deficiencies. Although the holotrichous condition is prevalent among taxa of Zerconidae, there are some taxa whose deutonymphs and adults are characterized by a few setal losses (Table 4). These losses have often not been recognized or emphasized as apparent apomorphies in the diagnoses of taxa. On the podonotum, setae s1 are present in a variety of apparently earlier derivative genera such as Syskenozercon, Halozercon, Parazercon, Parhozercon, Aspar and Skeironozercon, but they are absent in nearly all other genera including Zercon. Setae sl also are absent in some species of Zercon, and setae r1 (these may possibly be s1), s2 and z3 are absent in the monotypic genus Monazarcon. Setal pair z6 is singularly absent in Parazercon radiatus. All of these cases of absences involve setae that first appear in the deutonymph. This is not surprising, as deutonymphal setae are known to be generally less stable than setae that are first expressed in the larva or protonymph among other families of Gamasina (LINDQUIST & EVANS, 1965). The consistent location of setae r3 on the peritrematal shield of adults and the consistent retention of setae r1 may be plesiomorphies for the family Zerconidae, though perhaps they are apomorphies for the superfAMILY Zeronoidea (MORAZA & LINDQUIST, in press).

On the opisthonotum, absences of setae are confined to the J-series and to one of the posteriormost pairs of the R-marginal series (Table 4). The absence of setae J5 in Parazercon radiatus and the monotypic genus Parhozercon may be a synapomorphy between these taxa. Setal pair Z2 is uniquely absent in the monotypic genus Monazarcon. Setae J2 are absent in the monotypic genus Skeironozercon, and both J2 and J4 are absent in Echinozercon orientalis (BLASZAK, 1976), though they are present in other species described in that genus (BLASZAK, 1982). As setae R7
may or may not occur in various genera of Zerconidae, their presence or absence seems to be a homoplastic condition of little value in definition of genera.

Neotrichy. Clarification of idiosomal setal homologies among zerconid mites in this study has been based on holotrichous exemplars, *i.e.*, on species characterized by the presence of all, or nearly all, of the setae normally present in the Gamasina, a natural group to which this family belongs. In holotrichous exemplars, these setae are idionymous, *i.e.*, they can be individually recognized and denoted on the basis of homology. In a few taxa of Zerconidae, however, deutonymphs and adults are characterized by a greater or lesser degree of idiosomal neotrichy. In some cases all setae remain idionymous, with the additional setae usually restricted to the opisthontonal shield where they are interspersed with holotrichous elements of the *R*-series and sometimes the *S*-series. Species of *Caurozercon* Halas'kova and *Echinozercon* Blaszak, with symmetrically doubled numbers of setae along the margins of the opisthontonal shield of deutonymphs and adults, are cases in point (HALASKOVA, 1977; PETROVA, 1979; BLASZAK, 1982) (Figs. 19A, 22); these are examples of oligotrichy or costriotrichy, as distinguished by GRANDJEAN (1965). In a few other cases neotrichy is more extensive, and additional setae are found on both the podostomal and opisthontonal shields; some setae are paired and others not, such that they are mostly adelonymous *sensu Van der Hammem* (1975). Species of *Syskenerzercon* and *Halozzercon* have extensive neotrichy on both shields; the setae are symmetrically multiple marginally but asymmetrical and haphazardly

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**Figures 23-24:** Idiosomal dorsum of *Aspar anisotrichus* Halaskova, showing ontogenetic changes in position of setae Z3-Z4 (redrawn and modified from Halaskova 1977). 23. — Deutonymph. 24. — Adult female, with setae inserted on peritrematal shield shown to the side.
arranged centrally and midlaterally (ATHIAS-HENRIOT, 1976; WIŚNIEWSKI et al., 1992). These are examples of plethiotrichy sensu GRANDJEAN (1965), in which many of the setae show dissymmetry and variability in placement among individuals such that they can not be denoted meaningfully. In all cases published or otherwise known to us among zerconid mites, neotrichy is restricted to the podonotal and opisthonotal series of setae, and it does not involve the truly opisthogastric elements. Neotrichy may be evident to some extent laterally on the opisthogaster in Syskenozercon, Halozercon and Caurozercon, but this may be due to the fusion of the opisthonotal shield with the ventrianal shield, and to extension of the neotrichous R-marginal series onto that area. Syskenozercon and Halozercon are thought to be early derivative members of the family Zerconidae (ATHIAS-HENRIOT, 1976, MORAZA & LINDQUIST, in press). Whether neotrichy is an ancestral state of this family, however, is problematical in that this condition is not evident among other known members of the superfamily Zerconoidea (MORAZA & LINDQUIST, in press).

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